

Update on the genomics and basic biology of *Brachypodium*

International *Brachypodium* Initiative (IBI)

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The scientific presentations at the First International *Brachypodium* Conference (abstracts available at <http://www.brachy2013.unimore.it>) are evidence of the widespread adoption of *Brachypodium distachyon* as a model system. Furthermore, the wide range of topics presented (genome evolution, roots, abiotic and biotic stress, comparative genomics, natural diversity, and cell walls) demonstrates that the *Brachypodium* research community has achieved a critical mass of tools and has transitioned from resource development to addressing biological questions, particularly those unique to grasses.

A model for grass genome organization

This report highlights recent advances made in *Brachypodium* research, focusing on the use of *B. distachyon* and related species to understand biological processes. Its experimental and genomic tractability allow *B. distachyon* to act as a functional genomic test-bed to accelerate the improvement of grain, forage, and biomass crops. Its strengths as a model plant (e.g., short generation time, efficient *Agrobacterium*-mediated transformation, and availability of mutant collections) are described in [1] and other reviews

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published in the past 5 years. The main web portal for *Brachypodium* (<http://www.brachypodium.org>) contains a genome browser and links to community resources. In addition, two project-specific websites (<http://brachypodium.pw.usda.gov/> and <http://www-urgv.versailles.inra.fr/tilling/brachypodium.htm>) provide access to T-DNA and Tilling resources, respectively.

The compact nature of the fully sequenced [2] *Brachypodium distachyon* genome is a major reason for the success of *B. distachyon* as a model system, and provides unique opportunities to study various aspects of grass genome organization and evolution. Moreover, as a monocot reference, it permits comparisons of genomic landscape dynamics with the dicot model *Arabidopsis thaliana*. Thus, *B. distachyon* has become an appealing target for plant molecular cytogenetics.

One of the most informative cytomolecular tools is chromosome painting (CP), which enables unique and unambiguous visualization of individual chromosomes or large segments, both during cell division and even at interphase, using fluorescence *in situ* hybridization with specific DNA probes. CP was initially applied to vertebrate systems. Whole-genome sequencing (WGS) and large-insert genomic DNA libraries allow its application to small-genome plants such as *A. thaliana*. The sequencing of the *B. distachyon* genome [2] combined with its low (5) chromosome number and a well-developed cytogenetic infrastructure has allowed the CP of several *Brachypodium* species [3], a pioneering application of CP in monocots.

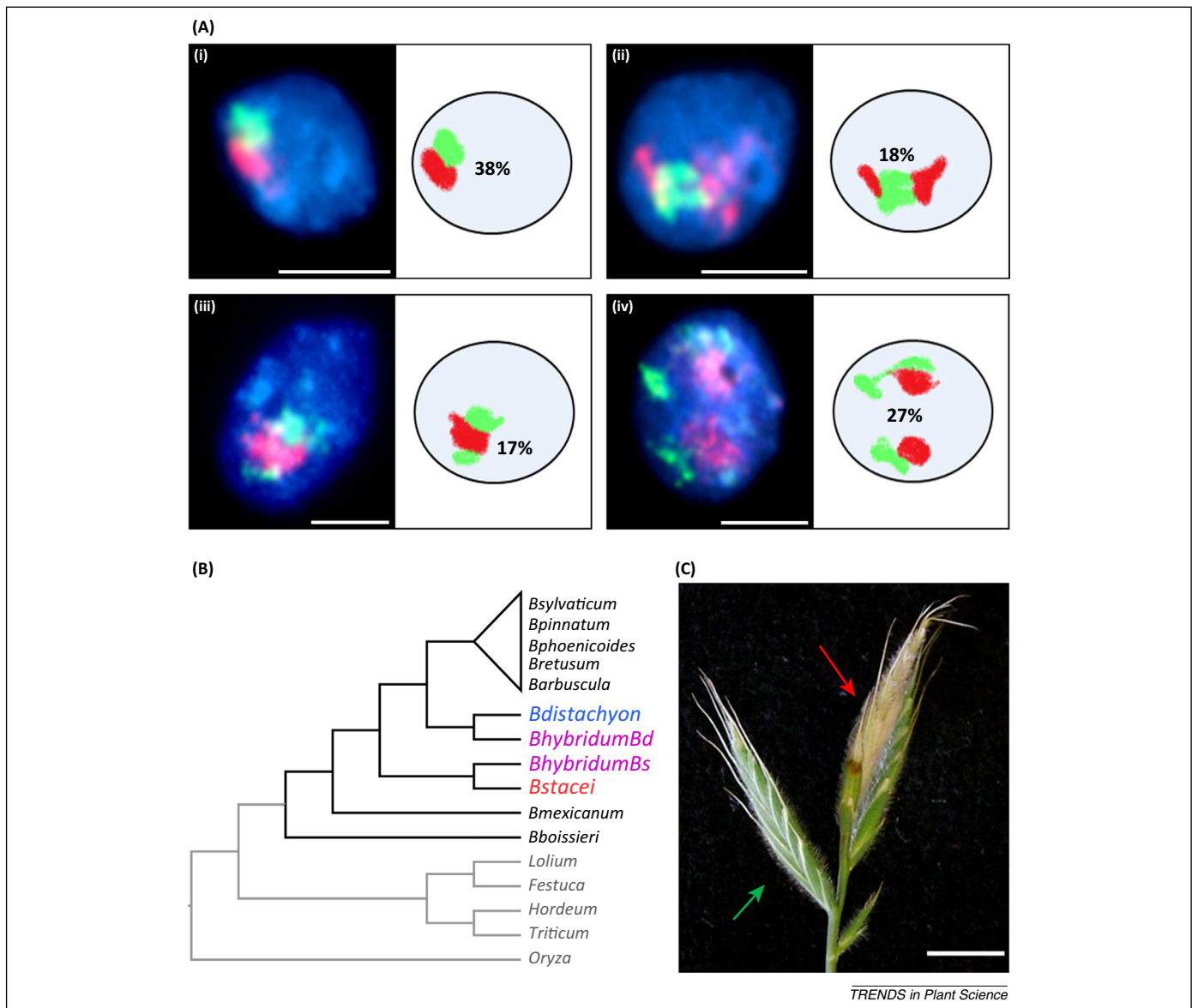


Figure 1. (A) Different arrangements of the Bd2 homologous chromosome territories (CTs) and the observed frequencies (%) of their occurrence in interphase nuclei of roots of *B. distachyon*: (i) complete association; (ii) top (green fluorescence) and (iii) bottom (red fluorescence), arm-only association; (iv) complete separation. Chromatin stained with DAPI (4',6-diamidino-2-phenylindole; blue fluorescence). Scale bars: 5 μ m. For better visualization the respective arrangements of CTs have been schematically shown on the diagrams next to photomicrographs. Documentation courtesy of Ewa Breda (University of Silesia in Katowice, Poland). (B) Evolution of the three *B. distachyon*-complex species. Summarized low-copy nuclear GIGANTEA (G1) gene tree showing the phylogenetic reconstruction of *B. stacei*, *B. distachyon*, and *B. hybridum* [*B. hybridum* shows G1 copies from both stacei-type (BsBs genome) and distachyon-type (BdBd genome) parents, coinherited from bidirectional crosses]. (C) *Fusarium* head blight symptoms on Bd21 spikes following point inoculation (red arrow) with *Fusarium graminearum* strain FgUK1 at 6 days after inoculation. An asymptomatic spike (green arrow) is shown for comparison. Scale bar, 1 cm. Photograph courtesy of Paul Nicholson and Antoine Peraldi (John Innes Centre, UK).

The chromosomes of *B. distachyon* can be selectively painted to address important questions about grass genome structure and evolution (in Figure 1 we demonstrate how they are arranged at interphase). CP of *B. distachyon* chromosome 2 (Bd2) in the nuclei of root cells revealed that Bd2 homologous chromosome territories can assume four different configurations that are observed at different frequencies (Figure 1A). This is one example where research in *Brachypodium* could lead the way in determining whether and how nuclear structure is linked to cell differentiation and tissue-specific gene expression.

A tractable model for inter- and intraspecific diversity

The genus *Brachypodium* contains 15–18 species with unusually variable chromosome numbers and ploidy

levels. This diversity was a subject of interest long before *B. distachyon* became a model grass. WGS of *B. distachyon* [2], together with the advent of inexpensive next-generation sequencing (NGS) technologies, set the stage for high-resolution investigation of the genomic diversity and evolutionary relationships in the genus.

It was recently demonstrated that '*B. distachyon*' is a complex of three separate species: two diploids (*B. distachyon*, *B. stacei*) and their derived allotetraploid (*B. hybridum*) ([4] and Figure 1B). The genomes of *B. stacei* and *B. hybridum* are being sequenced, and gene expression is being compared between all three species, to serve as a model for speciation through adaptation and polyploidization. To develop further this trio of species as a model for plant polyploidy, allopolyploids are being developed

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